

**AUSTRALIAN FOSSIL PENGUINS,
WITH REMARKS ON PENGUIN EVOLUTION AND DISTRIBUTION**

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Fig. 1-6

INTRODUCTION

A fossil penguin bone from Australia was first described by Finlayson in 1938. Since then three other specimens have been found. Glaessner (1955) has discussed the stratigraphy and biostratonomy of all four occurrences and has figured two of the more recently discovered bones. The four specimens were then referred to me for morphological and systematic study, which is the subject of the present paper. The specimens are the property of the South Australian Museum, and I am much indebted to the authorities of that Museum and to Dr. M. F. Glaessner of the University of Adelaide for the opportunity to study them.

The four Australian specimens come from two horizons, late Eocene and Oligocene. None is surely identifiable to species, but they represent at least three species. One Eocene specimen is identifiable to genus, *Palaeudyptes*. The other Eocene specimen may be of the same genus and species. The two Oligocene specimens are certainly of different species and probably genera, one a palaeudyptine and the other not placeable as to subfamily.

Since I reviewed the whole subject in 1946, additional discoveries of fossil penguins have been made not only in Australia but also in New Zealand and Antarctica. Several further studies on penguin paleontology and evolution have been published, notably the outstanding work of B. J. Marples (1952, 1953). Another full review is not now called for, but this occasion is taken to append an up-to-date summary of fossil penguin distribution and two brief notes on a morphological point and on a criticism of a theory of penguin origins.

In tables of measurements (Tables 1-3), I have numbered the dimensions as in Marples (1952, 1953) to facilitate comparisons. All measurements are in millimeters.

The accompanying drawings are by Chester Tarka.

DESCRIPTIONS OF SPECIMENS

Palaeudyptes cf. antarcticus

THE EOCENE HUMERUS

(Fig. 1.)

Specimen. S. A. M. No. P7158, left humerus, nearly complete but with salient parts of both ends eroded. Collected by W. Burdett.

Locality. Witton Bluff, at the southern end of Christie's Beach, about 16 miles south of Adelaide.

Horizon and Age. "Transitional Marl" member, which forms the base of the Blanche Point Marls, late Eocene (Glaessner, 1955).

Previous Publication. This is the specimen summarily described and figured in external and postaxial aspects by Finlayson (1938). Marples (1952) compared a cast with New Zealand specimens, but made only a generalized statement of similarity, without description or figure. Simpson (1946) discussed the specimen briefly on the basis of Finlayson's figures, and Glaessner (1955) has discussed its occurrence and age.

Description. This is a large, but not maximal, fossil penguin humerus. Size and proportions are near those of the seven New Zealand humeri referred to *Palaeudyptes antarcticus* by Marples (1952), but most dimensions are at or slightly below the smallest measurements on Marples' specimens. The proximal part of the shaft is, however, relatively thick (dorso-ventrally). The shaft tapers from proximal to distal, very slightly but still somewhat more than is usual in the New Zealand specimens. See Table 1. There is no preaxial angle or tubercle.

The distal end is somewhat eroded and crushed or cracked, but seems to have been about as in *Palaeudyptes antarcticus* (Marples, 1952, Fig. 2, No. 3). The angle between the midline of the shaft and a tangent to the ulnar and radial condyles was probably between 25° and 30°. This is a difficult measurement to make consistently, even on perfect bones, and is consequently open to considerable error here, but the angle is certainly unusually low. 40° is the smallest angle noted for *Palaeudyptes* by Marples, but on some of his illustrations I obtain values as low as 30° or slightly less, which suggests that our technique differs. In any case both this bone and New Zealand *Palaeudyptes* have low angles and there is insufficient evidence of significant difference between them.

The head is characteristically palaeudyptine, without apparently distinctive characters within that group. The same is true of the tricipital fossa, which is completely undivided and is small relative to the bulk of the whole bone (a point separately discussed later in this paper). There is no angle or prominence on the preaxial border, a feature

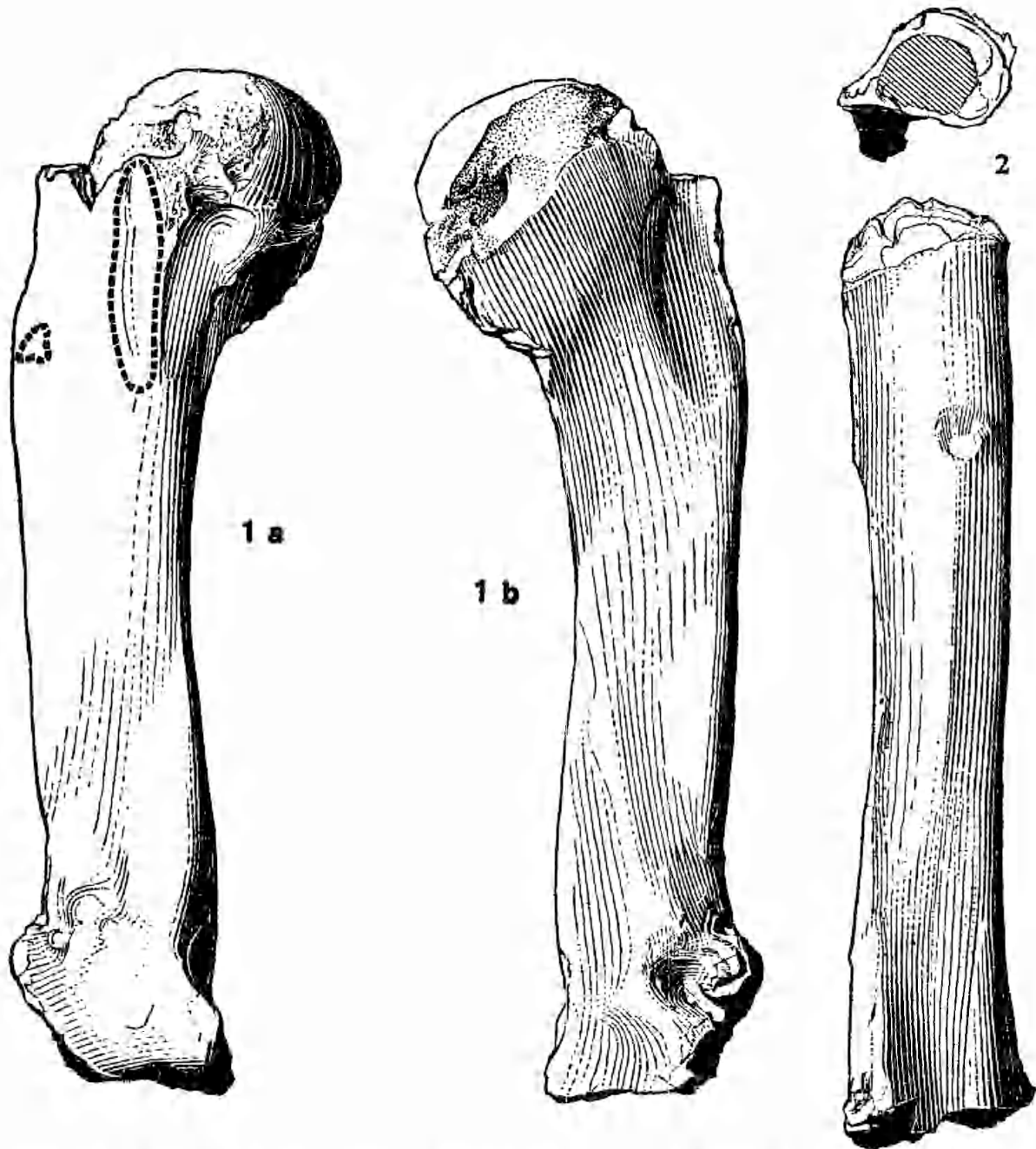


Fig. 1. *Palaeudyptes* cf. *antarcticus*. S.A.M. No. PT158, left humerus. a, ventral aspect. b, dorsal aspect. Insertions of *pectoralis secundus* and *latissimus dorsi* are marked by heavy broken lines. Cracks in shaft have been omitted and small missing fragments restored, but eroded parts of proximal and distal ends have not been restored ($\times 3$).

Fig. 2. *Palaeudyptes* cf. *antarcticus*? S.A.M. No. 10862, shaft of right tibio-tarsus. Proximal view, showing cross section at break, and posterior view. Cracks have been omitted and small fragments missing from shaft have been restored ($\times 2$).

constant in recent penguins, absent or slight in New Zealand *Palaeudyptes*, but present in some other palaeudyptines.

The insertion of the *pectoralis secundus* is not well defined, but it is evidently nearly parallel with the shaft and it is well separated from

the small *latissimus dorsi* insertion—characters typical of the early penguins and specifically of *Palaeudyptes antarcticus* although somewhat variable in the latter. There is a marked depression or small fossa between the proximal end of the *pectoralis secundus* insertion and the lip of the tricipital fossa (near and proximal to the insertion of the *pectoralis tertius*).

The capsular groove is not perfectly preserved or completely freed from matrix. It may, doubtfully, be a little less sharply defined or continuous than in New Zealand *Palaeudyptes* and to that extent more like recent penguins.

Classification. Finlayson (1938) pointed out the close resemblance of this bone to *Palaeudyptes antarcticus* of New Zealand but did not make a definite identification. Marples (1952) compared a cast with the New Zealand specimens and confirmed the resemblance except for the slightly smaller ("more slender") size of the Australian humerus. He referred to it as *Palaeudyptes* sp., as I (Simpson, 1946) had previously done from Finlayson's published data, alone. The bone obviously belongs to the Palaeudyptinae (Simpson, 1946, usefully redefined by Marples, 1952 and 1953). It cannot be distinguished generically from *Palaeudyptes*. It has slight and somewhat dubious apparent differences from New Zealand specimens of *P. antarcticus*, as noted above. These are no greater than variations that commonly occur within a single species, and they do not warrant designation of a new species. Nevertheless the possible slight morphological differences and the markedly different provenience prevent a fully positive assignment to *P. antarcticus*. The most reasonable identification at present is *Palaeudyptes* cf. *antarcticus*.

Table 1.
COMPARATIVE MEASUREMENTS OF HUMERI

	P7158	P10863	<i>P. antarcticus</i> (Marples)
1. Extreme length	154	—	159-172(2)**
2. Head to angle at base of dorsal sesamoid groove	152	—	153-166(4)
3. Distal end of insertion of <i>pectoralis secundus</i> to angle of 2	ca. 100	—	104-117(6)
4. Head, greatest diameter	ca. 45	ca. 53*	46-49 (5)

5. Pre-postaxial diameter of shaft $\frac{1}{3}$ distance from head	28 $\frac{1}{2}$	29	28-35 (7)
6. Same, $\frac{2}{3}$ distance from head	25 $\frac{1}{2}$	ca. 29	28-35 (6)
7. Dorsoventral diameter of shaft $\frac{1}{3}$ distance from head	13	14	11 $\frac{1}{2}$ -13 (6)
8. Same, $\frac{2}{3}$ distance from head	11 $\frac{1}{2}$	ca. 14	12-14 (6)
10. Preaxial side of radial condyle to longest distal process	ca. 40	—	45-50 (4)
11. Transverse diameter of distal end across ulnar condyle	ca. 18	—	18-21 (5)

*47.3 as preserved, about 5 $\frac{1}{2}$ mm. believed to be eroded.

**Figures in parentheses are numbers of specimens measured by Marples.

***Palaeudyptes cf. antarcticus* ?**

THE EOCENE TIBIOTARSUS

(Fig. 2)

Specimen. S. A. M. No. P10862, right tibiotarsus, lacking both ends and with shaft somewhat broken. Collected by M. F. Glaessner.

Locality. North of Port Noarlunga jetty, at the base of the cliff extending southward from Witton Bluff, at high water level.

Horizon and Age. Just below the top of the Banded Marl member of the Blanche Point marls, about 20-25 feet above the transitional marl (in which P7158 was found), late Eocene (Glaessner, 1955).

Previous Publication. Listed but not described or figured by Glaessner (1955).

Description. This tibiotarsus is slightly smaller than that referred to *Palaeudyptes antarcticus* by Marples (1952), and hence is from an animal of the same size as the humerus described above. Few distinctive characters are preserved. The shaft is flattened dorsoventrally and is rounded, with a sharp crest only at and below the region of contact with the fibula. To the extent that they differ from recent penguins, these characters are common in the older fossil penguins and especially in the *Palaeudyptinae*.

Classification. Positive identification is hardly possible, but as far as it goes the bone is entirely consistent with reference to *Palaeudyptes*. Difference in age from the humerus of *Palaeudyptes* cf. *antarcticus* is not likely to be significant, and the fact that the two animals were of almost exactly the same size establishes a certain presumption that they were of the same species.

Table 2.

COMPARATIVE MEASUREMENTS OF TIBIOTARSI

	P10862	<i>Palaeudyptes antarcticus</i> (Marples)
2. Pre - postaxial diameter $\frac{1}{3}$ length from proximal end	ca. 24	28
3. Same, $\frac{2}{3}$ length	ca. 19	23
4. Dorsoventral diameter $\frac{1}{3}$ length from proximal end	ca. 16	16
5. Same, $\frac{2}{3}$ length	ca. 14½	16

Gen. et sp. indet., A

THE OLIGOCENE HUMERUS

(Fig. 3)

Specimen. S. A. M. P10863, right humerus without distal end and with proximal end heavily eroded. Collected by M. Pritchard.

Locality. Pritchard Brothers' building-stone quarry about 7½ miles west-northwest of the town of Mt. Gambier.

Horizon and Age. Gambier limestone, Oligocene (Glaessner, 1955).

Previous Publication. Figured and tooth marks discussed by Glaessner (1955).

Description. The humerus when complete was at least as large as *Palaeudyptes antarcticus*, but of somewhat different proportions. The badly eroded head nevertheless indicates that this part was larger than in *P. antarcticus* both absolutely and in proportion to the transverse diameters of the shaft. The *pectoralis secundus* insertion is only very slightly oblique, well separated from the *latissimus dorsi* attachment, and the fossa between it and the lip of the tricipital fossa is shallow. There is a distinct preaxial tubercle or angle, and the contour of the shaft proximal to this is concave, making this slightly the narrowest part of the shaft, which nevertheless has nearly parallel sides and does not seem

to have been notably sigmoid. The tricipital fossa is narrow and undivided. Measurements are included in Table 1.

Classification. This specimen is quite surely palaeudyptine, but it cannot be referred with assurance to any named genus in which the humerus is known. The size of the species is probably in the range of

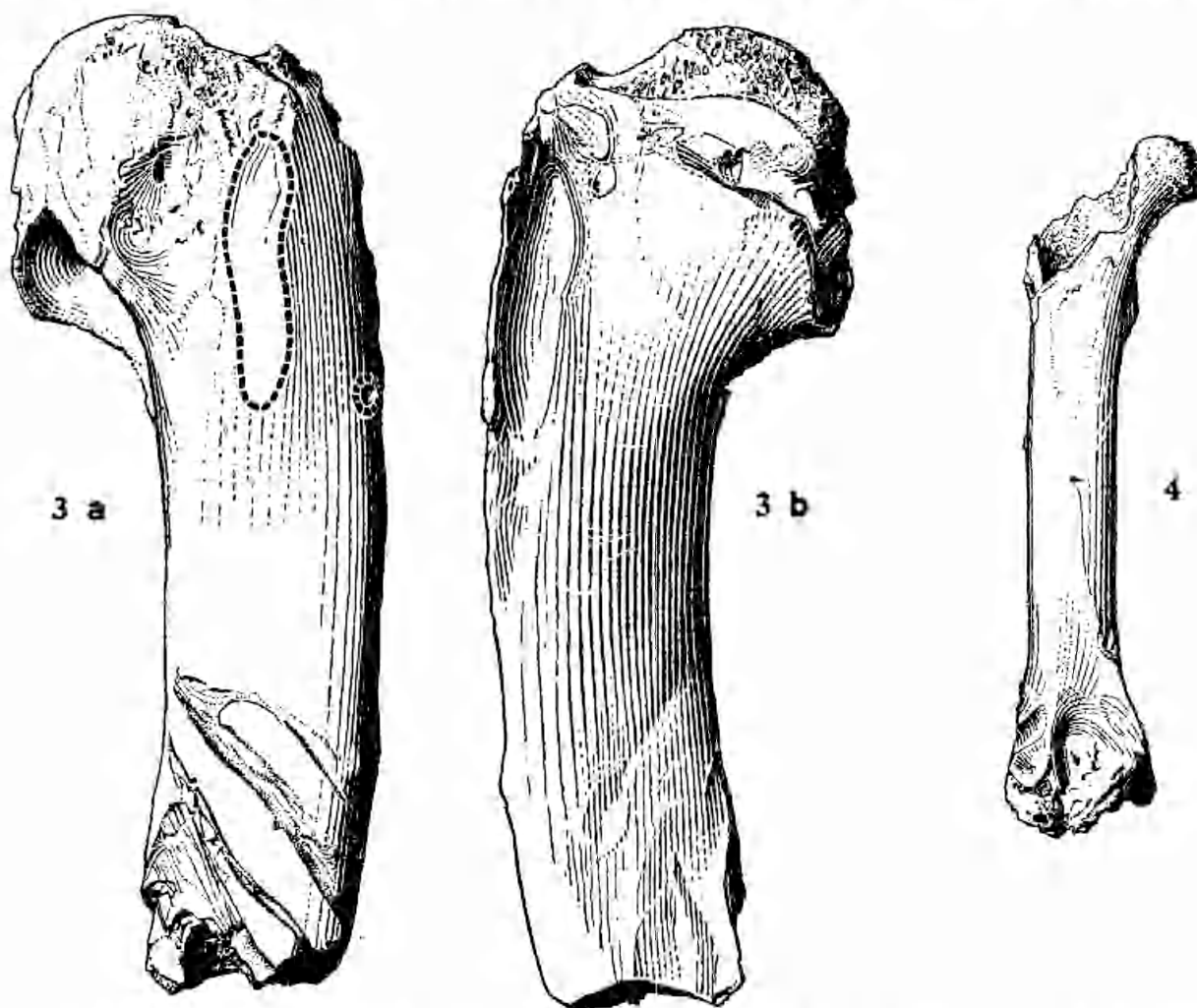


Fig. 3. Gen. et sp. indet., A. S.A.M. No. P10863, part of right humerus. a, ventral aspect. b, dorsal aspect. Insertions of *pectoralis secundus* and *latissimus dorsi* are marked by heavy broken lines. Cracks in shaft have been omitted and small missing fragments restored, but imperfections of proximal and distal ends are as shown. Apparent tooth marks on disto-ventral part are shown (x8).

Fig. 4. Gen. et sp. indet., B. S.A.M. No. P10870, imperfect left femur. Posterior (or ventral) aspect. No restoration (x8).

Palaeudyptes antarcticus, but it differs from *Palaeudyptes* especially in the relatively larger head and the prominent preaxial tubercle. *Pachydyptes* has a much stouter, stockier humerus and a smaller tubercle with the contour convex above it. *Platydyptes* and *Archaeospheniscus* have the *pectoralis secundus* insertion more oblique, and the latter genus also has a smaller tubercle and less concave contour above it. The Seymour Island *Anthropornis* is generally rather similar but has a relatively

smaller head and stouter shaft and a smaller preaxial tubercle. *Eosphaeniscus*, also from Seymour Island, has a heavily accented fossa between the *pectoralis secundus* and the tricipital fossa, quite different from the present specimen.

Few and slight as these differences are, they are just such as to distinguish the humeri of defined genera of palaeodyptines. It is therefore improbable that this specimen belongs to the same genus as any previously described humerus. Nevertheless it seems inadvisable to base a new generic or specific name on this inadequate type, which might make difficult or impossible the exact identification of future finds, especially because the length of the shaft and the important characters of the distal end are unknown. There are, furthermore, several named palaeodyptine genera in which the humerus is unknown and to which, therefore, this bone might conceivably belong. It is designated only as *gen. et sp. indet.*, with the comment that it is not the same as the late Eocene form described above, and that it is also of a different species, and doubtless genus, from the contemporaneous femur next described.

Gen. et sp. indet., B

THE OLIGOCENE FEMUR

(Fig. 4)

Specimen. S. A. M. No. P10870, left femur, lacking the trochanter and the distal end and with the head badly eroded. Found by D. J. Leonard.

Locality. Found in a block of building stone, from the vicinity of Mt. Gambier.

Horizon and Age. Gambier limestone, Oligocene, (Glaessner, 1955).

Previous Publication. Figured, without description, by Glaessner, 1955.

Description. The femur in penguins is not a very distinctive bone, and this specimen has lost just those parts that might have been most characteristic. The shaft is rather stout, although probably no more so than would be expected in average penguins of this size. Although the trochanter is lacking, the contour of the shaft below it suggests that it was less compressed laterally, or displaced medially, than in recent penguins—a feature common in the Miocene and older penguins. The shaft is nearly smooth except for a prominent rugosity just below the head and the usual, not especially prominent, ventral ridges above the condyles. The animal was slightly below the mean size of the living *Aptenodytes patagonicus*. (See Table 3.) Glaessner suggested that the trochanter had been bitten off, but there are no clear tooth marks.

Classification. This bone is unidentifiable, even as to subfamily, both because it lacks characteristic parts and because most genera and species of fossil penguins are known from and defined by the tarsometatarsus and the humerus and not the femur. This femur is much too small to be conspecific with any of the three specimens described above, and indeed the discrepancy suggests that it is not congeneric with any of them. All one can say now is that at least two quite distinct penguins, one a palaeodyptine and the other of unknown subfamily, are present in the Gambier limestone.

Table 3.

MEASUREMENTS OF FEMUR

P10870

1. Notch between head and trochanter to notch between condyles	ca. 90-95 (very rough approximation).
2. Greatest proximal width	ca. 22
5. Pre-postaxial diameter at middle of shaft	11½
6. Dorsoventral diameter at middle of shaft	11½

NOTE ON RELATIVE SIZES OF THE TRICIPITAL FOSSA

Wiman (1905), Finlayson (1938), and Lowe (1939) stated, on the basis of New Zealand, Australian, and Seymour Island fossils, that their tricipital fossae are smaller, relative to the size of the whole humerus, than in living penguins. I (Simpson, 1946) agreed that this is probably true of some, at least, of the larger fossil species, but pointed out that it is not true of smaller Patagonian fossils, notably in the genus *Palaeospheniscus*.

Marples (1952) made measurements for five New Zealand fossils, referred to four genera and species, and for one specimen each of seven recent species in five genera. The volumes were compared by filling the fossa with fine sand, the weight (W) of which was taken as directly proportional to the volume. The size of the humerus was measured as diameter of the head (D) and length of the whole bone (L). The indices $100 (W/D)$ and $100 (W/L)$ were then calculated and compared. These figures suggest, and Marples concluded, that the larger humeri have not only absolutely but also relatively larger fossae, contrary to the previous conclusions cited above. The evident further implication is that the differences depend on size and have no independent taxonomic value, or no bearing on evolutionary change other than size. It may be noted

that Marples' own figures show that the only recent species included in the comparison that are comparable in size with any of the fossils do, indeed, have larger fossae than the latter (see last column of Table 4). He concluded, however, that the species in question, *Aptenodytes forsteri* and *A. patagonicus*, "are clearly not typical penguins in this respect".

A valid index of relative size requires that "size" have the same number of dimensions in both terms of the comparison. Although less precisely quantitative, the comparisons involved in the statements about the tricipital fossa by Wiman, Finlayson, Lowe, and me were valid in that linear (one-dimensional) measurements of fossa and humerus were compared. The indices 100 (W/D) and 100 (W/L) are invalid because W is (indirectly) three-dimensional but D and L are one-dimensional. An index three-dimensional in both terms can be obtained by using the ratios W/D^3 or W/L^3 .

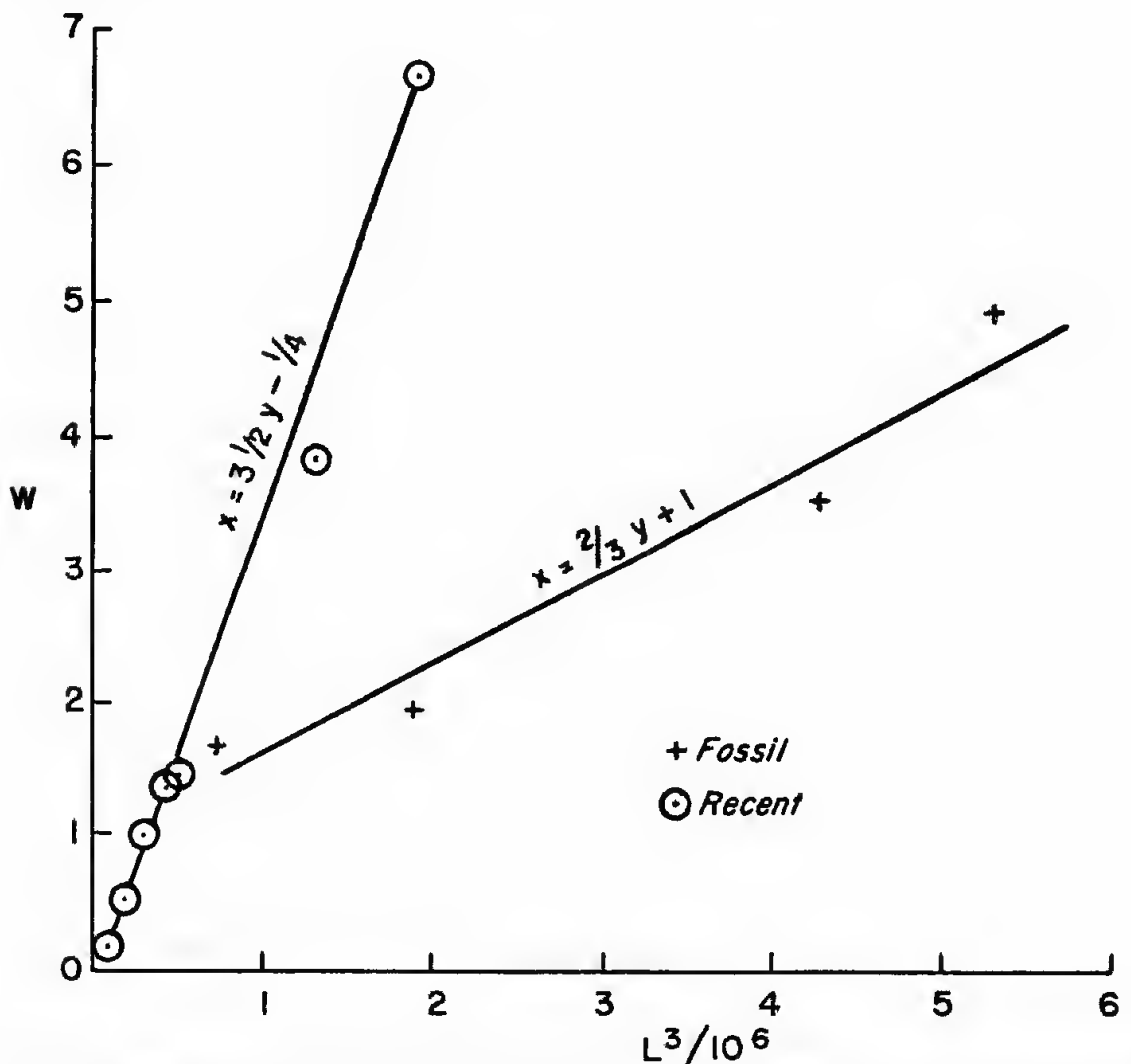


Fig. 5. Correlation of length of humerus and the index $10^6 (W/L^3)$ in some recent and fossil penguins. For fuller explanation see text. Raw data from Marples (1952).

Use of W to represent volume of the fossa depends on the relationship,

$$W = SV$$

where W is the weight of sand, V is the volume (three dimensional, of course) of the fossa, and S is the specific gravity of the sand-air aggregate. S depends in a complex way on the mineral composition and the size and shape distributions of the sand used. Its value is unknown in this case, but since it was kept constant in Marples' study his comparisons are valid in this respect. Use of L^3 (or of D^3) to represent volume of the bone depends on the relationship

$$L^3 = aV$$

in which a depends in a complex way on the shape of the bone. The value of a must vary somewhat from species to species and even from one individual to another, but in all penguins the shape of the humerus is sufficiently stereotyped to keep the variation of a within rather narrow limits. In other words, it is a reasonable premise that L^3 and V have a high, positive, rectilinear correlation. The correlation of L and V cannot be rectilinear.

In order to bring the index into a convenient order of magnitude the ratio W/L^3 may be multiplied, not by 10^2 as in Marples' index, but by 10^6 (i.e., 10^2 cubed). The results from Marples' raw data are given in the third column of Table 4, and compared with Marples' index in the fourth column. The indicated conclusions differ from those of Marples. Except for *Eudyptula minor*, the index for these recent penguins shows no evident trend with size and rather little variation. Since only single measurements are involved, the variation shown could be merely sampling variance around the same mean for the six species, although it is likely that some differences among species occur. It is *Eudyptula*, not *Aptenodytes*, that appears "clearly not typical . . . in this respect". The meaning of the apparent aberrancy of *Eudyptula* is not clear. Marples notes (without further data) that the volume of the fossa is highly variable in *Eudyptula* and the only specimen available to me seems to have a fossa relatively about as large as in other recent penguins.

In the four fossil penguins compared, the relative size of the fossa is decidedly smaller than in "normal" recent penguins (all the compared species except *E. minor*), confirming the earlier conclusion rejected by Marples. The discrepancy is most marked for the three largest fossil species, all of which have approximately the same index, 0.90-1.06 as against 2.83-3.59 for recent species other than *E. minor*. The fossil *Archaeospheniscus lowei* is of almost exactly the same size as the living *Aptenodytes forsteri*, but the indices are 1.06 and 3.50, respectively. The

smallest fossil species compared, *Platydyptes novaezealandiae*, happens to have a larger index (2.23) than the other fossils. This isolated observation is insufficient to establish a tendency for smaller fossil species to have relatively larger fossae, but it is noteworthy that still smaller species of *Palaeospheniscus* clearly have relatively large fossae ⁽¹⁾. Note also, however, that if only three or four recent species had been included they might have suggested a trend that is evidently absent when the seven species are included. For instance, *E. pachyrhynchus*, *M. antipodes*, and *A. patagonicus* would have shown a regular decrease of the index with increasing size, and *E. minor*, *P. papua*, *A. patagonicus* and *A. forsteri* would have shown just the opposite, a regular increase of the index. (See Fig. 5.)

The data of Table 4 and the graph of Fig. 5 still do not strictly represent a valid regression or reveal a possible growth pattern, because the variate *L* appears (with different dimensions) in both terms of the comparison: *L* and $10^6 (W/L^3)$. The valid regression of *W* on $L^3/10^6$ ⁽²⁾ is shown in Fig. 6. The regressions for both the recent and the fossil penguins measured by Marples clearly tend to follow linear patterns, but the two regressions are decidedly different. The regression for the recent specimens does not suggest significant deviation from a straight line, and it is somewhere in the neighbourhood of $x = 3\frac{1}{2}y - \frac{1}{4}$. (That line is merely sketched in freehand and the approximate equation derived from it; the scanty data do not warrant more elaborate curve fitting.) It is noteworthy that *Eudyptula minor* also falls near this line, within the probable limits of sampling error, and that with this treatment no recent species seems to be "exceptional".

The fossil species do suggest that their regression is not straight, but there are only four individual sets of measurements, and departures from a straight line could be random. (Neither the fossil nor the recent regression is straighter on a log graph, and use of the allometric equation is not indicated.) The regression is somewhere in the general neighbourhood of the straight line $x = \frac{2}{3}y + 1$ (roughly sketched by eye, as for the recent data). Even with so few data, there can be no serious doubt that the regressions are very different for the recent and the fossil species being compared. It is also again clear that among the larger species the fossils have decided smaller tricipital fossae than the living forms.

⁽¹⁾ Because the specific gravity (S of preceding discussion) of sand-air aggregates must vary greatly and is unknown for the sand used by Marples, it is impossible for another worker to produce further data comparable with his. Direct, reproducible, and precise comparisons could be made from measurements of the volume of a liquid that can be held in the fossa and of the displacement of liquid by immersion of the whole bone, but such measurements have not been made.

⁽²⁾ As in the index $10^6(W/L^3)$, the term 10^6 is introduced only to keep the variates compared in the same order of magnitude. The form of the regression would of course be the same if 10^6 were omitted.

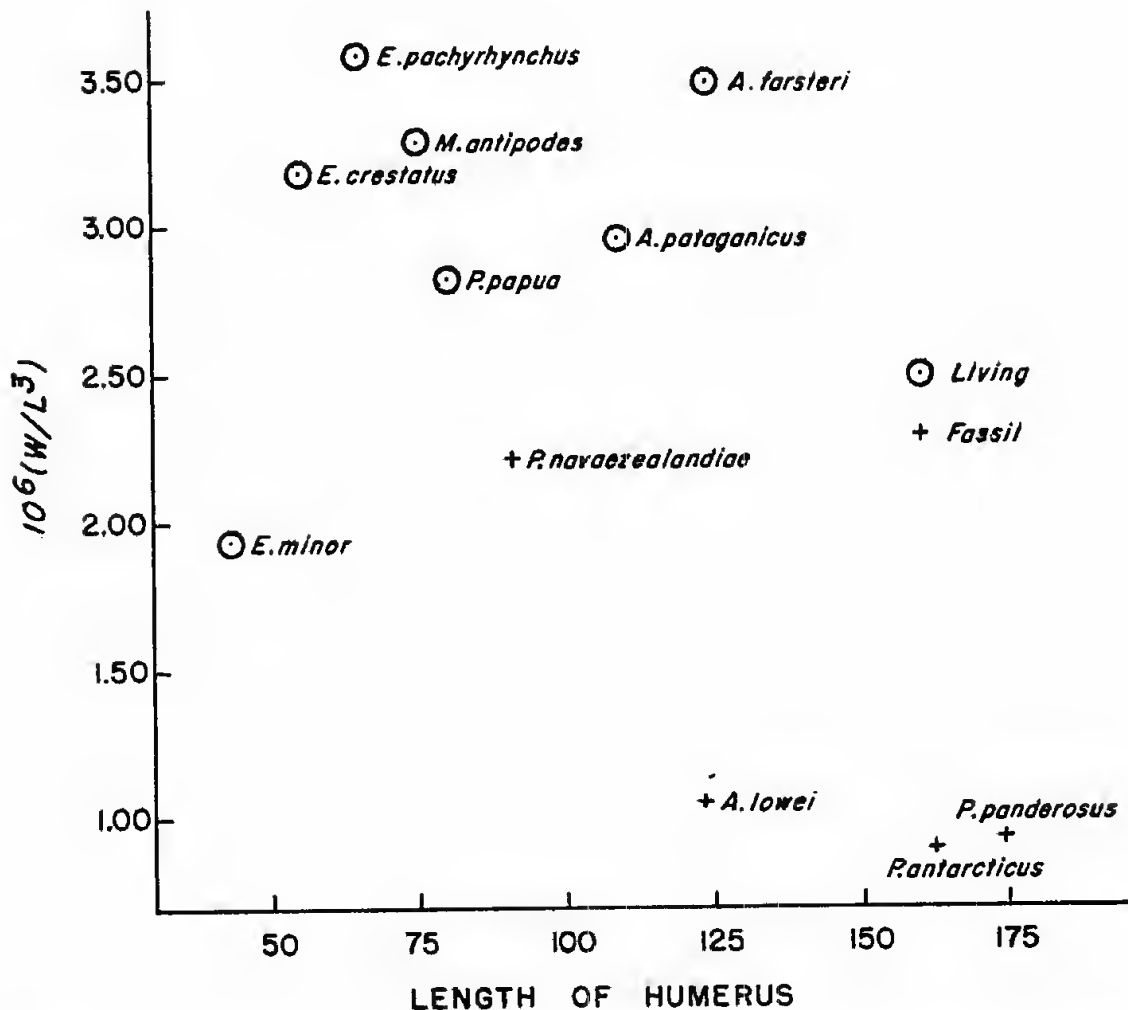


Fig. 6. Regression of W on $L^3/10^6$ for some recent and fossil penguins (species as in Fig. 5). For fuller explanation see text. Raw data from Marples (1952).

However, if an extrapolation of this regression should apply to other late Eocene to early Miocene penguins—an extrapolation not really warranted without further information—then the smallest of them would have tricipital fossae about equal to or even larger than those of recent penguins of the same size. It is suggestive, but no more than suggestive in the absence of precisely comparable measurements, that $L^3/10^6$ for the Patagonian fossil genus *Palaeospheniscus* (about 0.35-0.50 in various species) is in the region where the two regressions would intersect. As compared roughly by linear dimensions, that genus does indeed have tricipital fossae about as in recent penguins of comparable size.

Table 4.

RELATIVE SIZE OF TRICIPITAL FOSSA IN VARIOUS PENGUINS

(For explanation see text.)

Species:	Weight of sand (Marples) W	Length of humerus (Marples) L	Index $10^6(W/L^3)$	Index $10^2(W/L)$ (Marples)
Fossils:				
<i>Pachydyptes ponderosus</i>	4.91	174	0.93	2.8
<i>Palaeudyptes antarcticus</i>	3.81	162	0.90	2.3
<i>Archaeospheniscus lowei</i>	1.97	123	1.06	1.6
<i>Platydyptes novaezealandiae</i>	1.68	91	2.23	1.8
Living:				
<i>Aptenodytes forsteri</i>	6.68	124	3.50	5.3
<i>Aptenodytes patagonicus</i>	3.84	109	2.97	3.5
<i>Pygoscelis papua</i>	1.45	80	2.83	1.8
<i>Megadyptes antipodes</i>	1.39	75	3.29	1.8
<i>Eudyptes pachyrhynchus</i>	1.00	65.3	3.59	1.5
<i>Eudyptes crestatus</i>	0.53	55.0	3.19	0.9
<i>Eudyptula minor</i>	0.16	43.5	1.94	0.4

DISTRIBUTION OF FOSSIL PENGUINS

Fossil penguins are known from southern Argentina (Patagonia), Seymour Island ⁽³⁾, New Zealand, and South Australia. It was formerly believed that all occurrences were approximately contemporaneous, more or less early Miocene. Now Marples (1952) and Finlay (1952) have convincingly demonstrated that this is not true of the New Zealand specimens, and Glaessner (1955) has done the same for the Australian specimens. Although I have nothing new to contribute on this score, it will be convenient to review these newer data on penguin distribution, along with revised determinations which have not been gathered in any one publication.

New Zealand. Finlay (1952) identified and discussed microfossils associated with fossil penguins described by Marples (1952). The pertinent part of the provincial stage sequence and the ages assigned by Finlay are as follows:

(³) This occurrence is commonly called "Antarctic", but Seymour Island is not part of Antarctica and it is well north of the Antarctic Circle, at about 64° 15' south latitude.

Middle Oligocene	Waitakian— <i>P</i>
<hr/>	
	Duntroonian— <i>P</i>
Early Oligocene	Whaingaroan—? <i>P</i>
<hr/>	
	Runangan— <i>P</i>
Late Eocene	Kaiatan— <i>P</i>
<hr/>	
Middle Eocene	Bortonian
<hr/>	
Early Eocene	Heretaungan—? <i>P</i>

Penguins are most abundant in the Duntroonian, but occur also in the other stages marked with *P*. The scraps thought to be from the Heretaungan, unfortunately unidentifiable, are probably the oldest known fossil penguins. Good identifiable specimens occur from Kaiatan to Waitakian, late Eocene to middle Oligocene by Finlay's dating. Although known occurrences of most of the described species are confined to one stage or another, there seems to be no evident evolutionary progression and the single, most abundant species *Palaeudyptes antarcticus* is identified by Marples, on the basis of good specimens, for the whole range Kaiatan-Waitakian. (See Table 5.) This is a remarkably long span for a single species. I know of no other species and rather few genera of vertebrates present in both late Eocene and middle Oligocene. It is possible that more abundant collections would permit specific separation, but Marples' specimens suffice to show that there is, at most, little difference between earliest and latest occurrences referred to this species. One must conclude that the rate of evolution for *Palaeudyptes* had become effectively *nil* by late Eocene, that the Kaiatan-Waitakian span was shorter than Finlay indicates, or that some of the specimens are incorrectly dated.

Australia. The two older penguin bones described above are from the Blanche Point marls, formerly but incorrectly considered Miocene (Finlayson, 1938), in horizons now placed in or near the late Eocene. The younger bones are from the Gambier limestone, now placed in the Oligocene without, as yet, closer correlation. The age determinations by Glaessner (1955) are based mainly on still unpublished studies of foraminiferal faunas. In themselves the fossil penguins as yet are of no help in correlation, but the penguins known from the two ages are quite different, as shown above.

Patagonia. The stratigraphic position of the Patagonian fossil penguins is exactly known. With three dubious and probably erroneous claimed exceptions, all are from the base of the Patagonian formation ("Juliense" member). They are associated with "the richest and best known of all South American Tertiary faunas" (Feruglio, 1949), with extraordinarily abundant invertebrates as well as numerous sharks and whales. Despite all this knowledge, the age has been and still is disputed. It has been placed everywhere from early Eocene through Miocene. Nevertheless there is now a clear consensus that the age is late Oligocene or early Miocene, i.e., deposition occurred at or around the Oligocene-Miocene transition. The subject has been fully reviewed by Feruglio (1949).

Seymour Island. The Seymour Island penguins are presumably associated with a rather poor marine invertebrate fauna. Association *in situ* was rarely or not observed, but no marked age difference between the penguins and the invertebrates seems to be indicated. The invertebrate fauna has at least one species in common with the Patagonian formation, and is otherwise composed of distinct but closely allied species (review and references in Feruglio, 1949). On this basis it is highly improbable that these penguins are older than late Oligocene or younger than early Miocene. Marples (1952) pointed out that the Seymour Island penguins resemble the late Eocene-middle Oligocene forms of New Zealand, while (most of) the Patagonian penguins seem to be less primitive. He concluded that the Seymour Island forms may be older, belonging somewhere in the Oligocene (assuming the Patagonian to be Miocene). It is, however, to be remembered that: (a) no genera, *a fortiori* species, are known to be common to Seymour Island and New Zealand; (b) the apparent evolutionary rate of zero for at least one penguin of this general type from late Eocene to middle Oligocene (if the New Zealand dating is correct) suggests that still later survival of related and not identical forms would be more likely than not; and (c) the Patagonian penguin *Arthrodyles grandis* seems to be closely related to Seymour Island species. It seems probable that the marked difference between the Seymour Island and most of the Patagonian penguins is more a matter of facies than of age. (The localities are separated by some 20° of latitude and must both on this and on other accounts have had markedly different environmental conditions even in the Oligocene or Miocene.) On present evidence the Seymour Island penguins are not likely to have been appreciably older than the Patagonian, and might have been as late or even slightly later.

More recently Marples (1953) has revised the Seymour Island penguins, but without further discussion of their age.

Faunal lists. The known fossil penguins, according to the most recent revisions, are listed in Table 5.

Table 5.

KNOWN FOSSIL PENGUINS

A. New Zealand (data from Marples, 1952).

	Early Eocene	Late Eocene	Early Oligocene	Middle Oligocene
	Heretaungan	Kaiatan Runangan	Whaingaroan Duntroonian	Waitakian
Indet. x				
<i>Palaeudyptes</i>				
<i>antarcticus</i>	x	—	?	x
<i>Pachydyptes</i>				
<i>ponderosus</i>		x		
<i>Archaeospheniscus</i>				
<i>lowei</i>			x	
<i>A. lopdelli</i>			x	
<i>Duntroonornis</i>				
<i>parvus</i>			x	
<i>Platydyptes</i>				
<i>novaezealandiae</i>			x	?
<i>P. amiesi</i>			?	x
<i>Korora oliveri</i>				x

B. Australia (this paper).

	Age	
	Late Eocene Blanche Point marls	Oligocene Gambier limestone
<i>Palaeudyptes</i> cf. <i>antarcticus</i>	x	
Gen. et sp. indet. A.		x
Gen. et sp. indet. B.		x

C. Seymour Island (Wiman, 1905, and Marples, 1953).

(All of same age as far as known, probably late Oligocene or early Miocene.)

Anthropornis nordenskjoldi
Eosphaeniscus gunnari
Notodyptes wimani
Delphinornis larsenii
Ichthyopteryx gracilis (validity doubtful)

D. Patagonia (Simpson, 1946; some highly dubious records and probable synonyms omitted).

(All of same age, basal Patagonian, "Juliense" member, latest Oligocene or early Miocene).

Palaeospheniscus gracilis
P. rothi
P. patagonicus
Paraspheniscus bergi
P. nereius
Perispheniscus wimani
Isotremornis nordenskjoldi
Paraptenodytes antarcticus
P. curtus
Arthrodytes grandis
Arthrodytes? andrewsi

NOTE ON THE ORIGIN OF PENGUINS

I have elsewhere (Simpson, 1946) supported the theory that penguins arose, not from flightless land birds or in a delimited land area, but from diving sea birds (ecologically similar to diving petrels) widely distributed around the South Temperate Zone. Recently de Meillon (1952) has opposed all aspects of that theory on the evidence of penguin fleas.

The only fleas known to occur on penguins are *Listronius robertsianus*, *Parapsyllus longicornis*, and *P. magellanicus*. Both genera belong to the subfamily Parapsyllinae, with six other genera. Except for those on penguins (and other sea birds) all members of the subfamily are confined to South America where most of them are rodent fleas. De Meillon therefore argues that the penguins must have acquired the fleas in South America and must themselves have originated there. This seems to be a *non sequitur*. There is no evident reason why the penguins may not have acquired these fleas after penguins had evolved as such and had spread to South America from any place or zone of origin. As to why they happen to have *only* South American fleas (as far as known), that is no harder to explain on either theory, hence no better evidence for or against either, than the fact that they have long been in Australia and New Zealand (since the Eocene) and probably also in Africa (fossils unknown) without, apparently, acquiring parasites there. It is also pertinent that the earliest known penguins antedate the appearance of rodents in South America.

Moreover all three species of penguin fleas are known to occur also on wide-ranging groups of flying birds: *L. robertsianus* on petrels, *P. longicornis* on shearwaters and an Antarctic thrush, and *P. magellanicus* on whale-birds, jaegers, sooty albatrosses, albatrosses, and Cape pigeons. There is no evident reason why the primary dispersal of the fleas may not have been partly or wholly by flying birds.

De Meillon also implies that the abundance of fossil penguins in the South American "Subantarctic" (most of them are from far up in the Temperate Zone) supports his view. But, as noted above, known fossil penguins occur *earlier* in Australia and New Zealand. In fact the fossil record is so spotty that it does not really suggest anything about the place of origin except to conform with the idea that penguins have always been southern and to show that they were very widespread in the southern Temperate Zone by the end of the Oligocene.

De Meillon further argues that penguins probably arose as non-flying land birds because land birds are most likely to come in contact with rodents and flying birds would avoid the rodents by taking to the trees or to islands. But penguins do regularly come ashore on rodent-infested coasts, and probably have long done so. (The Patagonian fossil occurrences, at least, are near or at what was then a continental shore.) So do flying sea birds that could have transmitted fleas to penguins. Moreover, ground-nesting flying birds are very common in South America and elsewhere where rodents, and their fleas, are abundant.

De Meillon further cites in the same connection the tick *Ornithodoros talaje*, which occurs on South American rodents and, as a distinct subspecies, in South African penguin nests. But the same species is also known on terns, and the other known penguin ticks have almost certainly been acquired from flying sea birds (Zumpt, 1952). Moreover, however it occurred, the transfer of *O. talaje* from rodents to penguins probably took place relatively recently, millions of years after penguins first arose. Otherwise it is incredible that the ticks have moved to a new host and a new continent with only subspecific differentiation.

The evidence from parasites seems to me to have no special bearing one way or another on the origin of the penguins, and the theory earlier supported, although speculative, still seems most likely on other grounds.

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